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A wild strain of *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) from farm-stored maize in South Carolina: Development under different temperature, moisture, and dietary conditions ☆

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Abstract

The purpose of this study was to determine the duration of immature development and survivorship of *Plodia interpunctella* (Hübner) on maize over a range of temperatures and grain moisture contents encountered in maize stored on farms in the southeastern states (USA). Laboratory cultures were established with moths collected from farm-stored maize in South Carolina and maintained on cracked maize at 30 °C and 60% r.h. The incubation period and percentage hatch of eggs was determined at 18 combinations of temperature and r.h. Hatch was <1% at 15 and 40 °C. In the range 20–35 °C, percentage hatch declined as temperature increased, and the mean incubation period ranged from 3.1 to 8.5 d. Neither percentage hatch nor incubation period were affected by r.h. between 43% and 76%. The relationship between mean developmental period (oviposition to adult eclosion) and temperature was well described by a quadratic polynomial that predicted a decline from 67.6 to 30.1 d as temperature increased from 20 to 31.1 °C, followed by an increase to 38.5 d as temperature increased further to 35 °C. The results suggest a lower temperature threshold for development near 15 °C and an upper limit slightly greater than 35 °C. Moisture content had a significant effect on developmental period at all the temperatures studied, but the pattern of variation with moisture depended upon the temperature.

Keywords: Stored-product insects; *Plodia interpunctella*; Development; Survival; Stored maize

1. Introduction

Plodia interpunctella is a major cosmopolitan pest of granaries, food processing plants, warehouses, retail stores, and households; and the larvae are able to feed on a wide range of dried vegetable and animal materials including grain, cereal products, oilseeds, dried fruits, dried vegetables, nuts, and animal feed (Richards and Thomson, 1932; Cox and Bell, 1991). Although the effects of host commodity, temperature, and moisture on rate of development and survivorship of the immature stages are well documented (Prevett, 1971; Bell, 1975; Mbata and Osuji, 1983; Allotey and Goswami, 1990; Mbata, 1990; Johnson et al., 1992, 1995; Locatelli and Biglia, 1995; Locatelli and Limonta, 1998; Na and Ryoo, 2000; Perez-Mendoza and Aguilera-Peña, 2004), quantitative data sets sufficient for the development and validation of computer simulation models are lacking.

The purpose of the study reported here was to determine the duration of immature development and survivorship of *Plodia interpunctella* (Hübner) on maize over the range of temperature and moisture content encountered in maize stored on farms in the southeastern states of the United States of America. It was undertaken in concert with field studies of farm-stored maize in South Carolina (Arbogast and Throne, 1997; Arbogast and Chini, 2005) to provide quantitative data required for modeling the population

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dynamics of this moth and optimizing control strategies (Throne,1995).

2. Materials and methods

2.1. Temperature and humidity control

Constant temperatures of 15, 20, 25, 30, 35, and 40 ± 0.5 °C were maintained in six separate environmental rooms (Environmental Growth Chambers, Chagrin Falls, OH), each held at a constant relative humidity (r.h.) of 60 ± 5%. Constant relative humidities were maintained in clear polystyrene boxes (23 × 31 × 10 cm) (Tri-State Plastics, Latonia, Kentucky) by means of saturated salt solutions (Table 1) (Greenspan, 1977) prepared with reagent grade salts and distilled water. The water was brought to a boil on a stirring hot plate, the heat was turned off, and salt was added with continuous stirring until saturation was achieved. The saturated solutions were stored over salt in stoppered flasks at room temperature for 2–3 wk before use. They were then stirred thoroughly and poured over dry salt in the boxes to form a shallow slurry. Each box was provided with a latticed false floor with 13 × 13 mm openings (polystyrene eggcrate, Select Acoustic Supply, Concord, Ont.) to support insect cages and containers with maize samples. A mat of the same material was placed on the floor of each box to prevent splashing of the solutions.

Table 1
Equilibrium relative humidity over saturated salt solutions at various constant temperatures and equilibrium moisture content of the maize hybrid Pioneer 3320 held over these solutions

Salt	Temp. (°C)	Equilibrium r.h. (%)[a]	Equilibrium m.c. (%)	
			N	Mean ± SE[b]
K_2CO_3	15	43.2	—	—
	20	43.2	14	11.7 ± 0.05
	25	43.2	12	11.0 ± 0.03
	30	43.2	14	10.7 ± 0.04
	35	—	12	11.3 ± 0.13
	40	—	—	—
NaBr	15	60.7	—	—
	20	59.4	14	13.4 ± 0.04
	25	57.6	14	12.7 ± 0.02
	30	56.0	14	12.5 ± 0.03
	35	54.6	14	11.7 ± 0.03
	40	53.2	—	—
NaCl	15	75.6	—	—
	20	75.5	12	14.8 ± 0.06
	25	75.3	12	14.8 ± 0.04
	30	75.1	12	14.7 ± 0.03
	35	74.9	12	14.3 ± 0.04
	40	74.7	—	—

All maize samples reached moisture equilibrium in 49 d or less, and the means include all measurements made on the 49th day or later.
[a] Greenspan (1977).
[b] Equilibrium moisture content was not determined at 15 and 40 °C.

2.2. Maize

Pioneer 3320, a maize hybrid commonly grown in the southeastern United States, was used for rearing stock cultures and in all experiments. The equilibrium moisture content of this hybrid at various combinations of temperature and r.h. (Table 1) was determined by holding samples at constant temperatures over saturated salt solutions in constant humidity boxes and measuring the moisture content at intervals of 2–4 d with a Motomco Automatic Grain Moisture Tester Model 919 (DICKEY-john® Corp., Auburn, IL). Two samples in separate boxes were used for each temperature–humidity combination. Moisture determinations were plotted against time and were continued until the graph indicated clearly that the grain had reached equilibrium, which occurred in 49 d or less in all combinations. Measurements were continued for up to 65 d, and all readings at 49 d or more were pooled to calculate the mean (± SE) equilibrium moisture content at each combination.

2.3. Moth cultures

Cultures of *P. interpunctella*, established with moths collected from farm-stored maize in South Carolina, were reared on cracked maize at 30 ± 0.5 °C and 60 ± 5% r.h. in an environmental chamber. Each culture was contained in a 0.95-l jar covered with filter paper held in place by a lid with two holes (3 cm in diam.) for ventilation. Eggs were collected by confining recently emerged adults in a 0.95-l jar containing a piece of pleated black construction paper (to provide resting sites) and covered by a lid with 18-mesh wire screen. The jar was placed in a darkened box and eggs were collected after various periods of time by shaking them onto black construction paper. The collected eggs were surface-sterilized as necessary with 1% formalin to control granulosis virus before using them to set up new cultures. Fresh rearing stock was collected periodically from the storage bins to ensure that no moths were cultured for more than 12 generations.

2.4. Egg development

The incubation period and percentage hatch of eggs were determined at 18 combinations of constant temperature and relative humidity (Table 1). The cages used to study egg development consisted of clear acrylic blocks (22 × 12.5 × 1.2 cm) with fifty 0.96-cm holes bored through them. The bottoms of the holes were covered by a piece of fine-mesh nylon screen (mesh opening of 64 μ; Nitex, Sefar America, Depew, NY) glued to the underside of the block, and the whole block was supported on feet about 1 cm high. One egg was placed in each hole, which was then stoppered with a No. 2 cork. Observations were made daily

until the eggs hatched or died. The date of hatch was recorded and other events – marked indentation of the chorion (egg collapse), death of larvae within the egg, and death of larvae during hatching – were noted. Each combination of temperature and humidity was replicated three times, with each replicate set up on a different day with eggs from a different culture.

2.5. Comparative development on maize and a standard laboratory diet

Larvae were reared under nearly optimum temperature and moisture conditions for development (30 ± 0.5 °C and 60 ± 5% r.h.) in an environmental chamber, either on two kernels of maize split lengthwise or on a standard laboratory diet. The laboratory diet (Silhacek and Miller, 1972) consisted of ground dog meal (10%), rolled oats (4%), white cornmeal (26%), whole wheat flour (23%), wheat germ (2%), brewers' yeast (5%), glycerol (16%), and honey (14%). Eggs were collected and held in the environmental chamber, and newly hatched larvae (0–24 h) were collected for the experiment. Each larva was placed in a 16-ml sample bottle (Wheaton Science Products, Millville, NJ) with either split maize kernels or 1.85 g (the approximate weight of two split maize kernels) of the standard diet. The bottles were capped with polypropylene snap-on lids. A 2-cm-diam hole in each lid covered with a 200-mesh bronze screen disk (34% open area) (Hillside Wire Cloth Co., Passaic, NJ) provided ventilation. Single larvae were placed on one diet or the other in each of 200 bottles (100 bottles/diet). The two diets were arranged in alternating sequence on shelves in the environmental chamber, and observations were made daily to determine adult emergence. The adults were anesthetized with carbon dioxide, sexed, and weighed on an ultramicrobalance (Type UMT2, Mettler Instrument Corp., Hightstown, NJ) with readability to 0.0001 mg. Observations were continued until all the insects had either emerged or died.

2.6. Development on maize

The development of *P. interpunctella* on maize was studied at 12 combinations of constant temperature and relative humidity (Table 1) (Development was not studied at 15 or 40 °C, because almost no eggs hatched at these temperatures). For each combination, two split kernels (four pieces) of maize were placed in each of 100 sample bottles like those described in Section 2.5. Half of these bottles and a 300-g sample of whole maize kernels were placed in each of two constant humidity boxes in an environmental chamber. The samples were used to monitor moisture content of maize in each of the two boxes throughout the experiment by weekly determinations of the samples' moisture content. When the sample had reached moisture equilibrium (Table 1), one newly hatched larva (0–24 h old) was placed on the maize in each bottle. Larvae were obtained by collecting eggs over a 6-h period, confining them in cages with a small amount of cracked corn in a third constant humidity box, and checking them daily for hatch. The larvae were transferred to the sample bottles as they hatched. Preliminary experiments showed that the larvae bore into the kernel halves, making it difficult to observe their transformations without severely disturbing them, so observations were made only to determine the time of adult emergence. Observations were made twice a week until pupation began, then daily until all the adults had emerged. The adults were sexed and weighed within a day of emergence, or a day later if their wings had not yet fully expanded at the time of observation.

2.7. Statistical analysis

Statistical analyses were conducted with SigmaStat 3.1 and SigmaPlot 8.0 (Systat Software, Point Richmond, CA). Generally, raw data failed tests of normality and equal variance, and transformation of the data failed to correct this situation, so nonparametric tests were used. The Mann–Whitney rank sum test (rank sum test) was used to compare two groups. The Kruskal–Wallis ANOVA on Ranks (Kruskal–Wallis test) was used to compare more than two groups, followed by Dunn's test to make all pairwise comparisons. The Spearman rank correlation coefficient (R_s) was used to measure and test the significance of correlation. The X^2 test was used to test the significance of the difference between an observed sex ratio and an expected sex ratio of 1:1. Regression analyses were done with mean values of the dependent variables, which were normally distributed with equal variance. The median as well as the mean and SE were presented as descriptive statistics, because the distributions were skewed, making the median a better measure of location. Contours of median developmental period and percentage survival were drawn using Surfer 8 (radial basis functions, multiquadric function with default settings) (Golden Software, Golden, CO).

3. Results

3.1. Egg development

Percentage hatch, observed in batches of 50 eggs at temperatures between 20 and 35 °C, ranged from 45% to 100% (Table 2). Only 0.4% of eggs held at 15 °C hatched, although larvae were visible in 20.5% of those that did not; 0.2% hatched at 40 °C, but no larvae were evident in any of the unhatched eggs. In the range 20–35 °C, percentage egg hatch tended to decline as temperature increased (quadratic polynomial regression: adjusted $R^2 = 0.40$, $F_{(2,9)} = 4.7$, $P < 0.05$), but percentage hatch was not affected by r.h. at any temperature within this range (Spearman rank order correlation, $R_s = -0.16 - 0.64$, $P > 0.05$).

Table 2
Effect of temperature and humidity on egg development in *P. interpunctella*

Temp. (°C)	r.h. (%)[a]	Incubation period[b] (days)		Percentage hatch[c]		
		N	Mean±SE	Mean±SE	Min	Max
20	43.2	135[d]	8.5±0.05	90.5±5.5	79.6	96.0
	59.4	140	8.1±0.03	93.3±3.3	90.0	100.0
	75.5	131[e]	8.4±0.05	88.7±6.4	78.0	96.0
25	43.2	124	5.0±0.02	82.7±10.3	62.0	92.0
	57.6	132	4.9±0.03	88.0±2.0	86.0	92.0
	75.5	117	5.1±0.04	78.0±6.9	45.0	78.0
30	43.2	118	3.5±0.05	78.7±13.8	52.0	98.0
	56.0	121	3.1±0.02	80.7±5.2	72.0	90.0
	75.1	123	3.3±0.04	82.0±7.0	68.0	90.0
35	(43.2)	105	3.8±0.04	69.7±3.3	65.0	76.0
	54.6	(86)	3.7±0.05	(86.0±0.0)	86.0	86.0
	74.9	125	3.4±0.04	83.3±5.9	72.0	92.0

[a]Greenspan (1977). Value in parentheses estimated by extrapolation from lower temperatures.
[b]Based on the number of eggs (*N*) that hatched.
[c]Based on three replicates of 50 eggs each. Value in parentheses based on two replicates.
[d]One egg missing.
[e]Date of hatch unknown for two eggs.

The mean incubation period ranged from 3.1 to 8.5 d (Table 2). Kruskal–Wallis ANOVA showed significant differences ($P<0.01$) among the 12 combinations of temperature and relative humidity, and Dunn's test indicated that these differences were due to temperature ($P<0.05$).

Humidity had no significant effect at any of the four temperatures. The relationship between temperature and incubation period was well described by a quadratic polynomial (Fig. 1A) that predicted a decrease in incubation period from 8.3 to 3.2 d as temperature increased from 20 to 31.9 °C, followed by an increase to 3.6 d as temperature increased further to 35 °C.

3.2. Comparative development on maize and a standard laboratory diet

Comparison of developmental period and adult weight showed that the standard laboratory diet was superior to split maize kernels for development of *P. interpunctella* (Table 3). Males developed at the same rate as females on both the standard diet (rank sum test, $P = 0.91$) and split maize kernels ($P = 0.65$). Development (males and females combined) was significantly faster on the laboratory diet than on maize (rank sum test, $P<0.01$). Adult males weighed less than adult females on both the standard diet (rank sum test, $P<0.01$) and maize ($P<0.01$). Both males and females achieved a higher weight on the standard diet (rank sum test, $P<0.01$). The sex ratio did not differ significantly from 1:1 on either diet (laboratory: $\chi^2 = 0.83$, $P = 0.36$; maize: $\chi^2 = 1.92$, $P = 0.16$). Survivorship was 59% on the laboratory diet and 52% on maize.

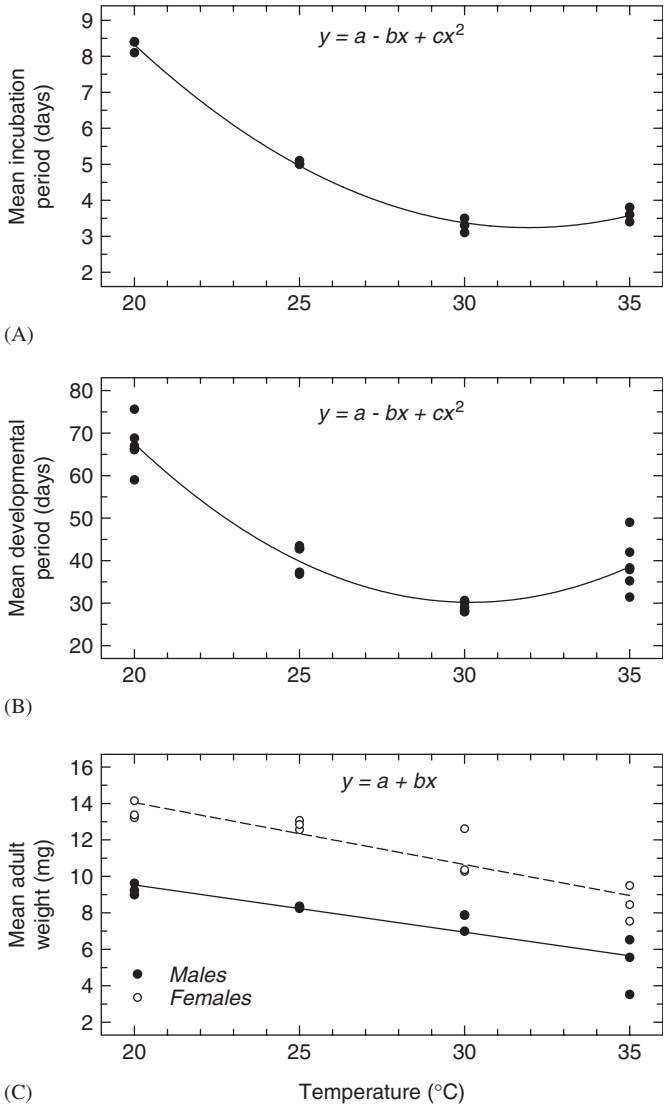

Fig. 1. Effect of temperature on development of *P. interpunctella*. (A) Mean incubation period of eggs: $Y = 39.6-2.28X+0.0357X^2$ (Adj. $R^2 = 0.99$, $F_{(2,9)} = 803$, $P<0.01$). (B) Mean period from oviposition to adult eclosion (males and females combined): $Y = 358-21.7X+0.360X^2$ (Adj. $R^2 = 0.92$, $F_{(2,21)} = 125$, $P<0.01$). (C) Weight of newly emerged adults: males, $Y = 14.7-0.259X$ (Adj. $R^2 = 0.75$, $F_{(1,10)} = 33.9$, $P<0.01$); females, $Y = 20.8-0.340X$ (Adj. $R^2 = 0.82$, $F_{(1,10)} = 50.6$, $P<0.01$).

3.3. Development on maize

Mean developmental period from oviposition to adult emergence ranged from 28.0 to 75.6 d (Table 4), and there was no significant difference between males and females under any combination of temperature and moisture content (rank sum test, $P>0.05$), except at 35 °C and 11.7% m.c. ($P<0.01$). The relationship between temperature and developmental period was well described by a quadratic polynomial (Fig. 1(B)) that predicted a decrease in developmental period from 67.6 to 30.1 d as temperature

increased from 20 to 31.1 °C, followed by an increase to 38.5 d as temperature increased further to 35 °C. Moisture content had a significant effect on developmental period (Kruskal–Wallis test, $P<0.01$) at all the temperatures studied, but the pattern of variation depended upon the temperature (Dunn's test, $P<0.05$).

Sex ratio did not differ significantly from 1:1 under any combination of temperature and moisture content ($X^2 = 0.00 - 1.35$, $P = 0.24 - 1.00$), with the exception of 35 °C and 11.7% m.c. ($X^2 = 23.21$, $P<0.01$).

Mean adult weight ranged from 3.520 to 9.114 mg in males and from 7.540 to 14.146 mg in females (Table 5). Females weighed significantly more than males at all combinations of temperature and moisture content (rank sum test, $P<0.01$), except at 35 °C and 11.3% m.c. ($P = 0.33$). Mean adult weight of both sexes declined at a constant rate as temperature increased (Fig. 1(C)).

The predicted response of development and survival to variation in temperature and grain moisture content is illustrated by the contour diagrams in Fig. 2. These diagrams indicate that the developmental period is minimal at 29–31 °C and 12.0–14.8% m.c. (Fig. 2(A)). It increases

Table 3
Development of *P. interpunctella* on a standard laboratory diet and on split maize kernels at 30 °C and 60% r.h.

	Laboratory diet				Split maize kernels			
	N	Median	Mean	±SE	*N*	Median	Mean	±SE
Duration[a]								
Males	26	23.0	23.6	0.2	31	28.0	28.5	0.3
Females	33	23.0	23.5	0.2	21	28.0	28.6	0.6
Weight[b]								
Males	26	8.955	8.900	0.199	31	7.610	7.553	0.139
Females	33	15.160	14.825	0.345	21	11.890	11.670	0.273

[a]Days from oviposition to adult eclosion.
[b]Weight (mg) of newly emerged adults.

Table 4
Developmental period (d) of *P. interpunctella* from oviposition to adult eclosion on split maize kernels

Temp (°C)	Moisture content (%)	Males			Females		
		N	Median	Mean±SE	*N*	Median	Mean±SE
20	11.7	50	66.0	67.0±0.7	46	66.0	66.1±0.4
	13.4	39	66.0	75.6±4.4	40	64.0	68.8±3.3
	14.8	45	58.0	59.0±1.0	40	60.0	66.2±4.2
25	11.0	40	41.5	43.5±0.9	32	41.0	42.8±1.0
	12.7	32	39.0	42.8±1.6	42	40.0	43.0±1.3
	14.8	46	37.0	37.3±0.5	43	36.0	36.8±0.3
30	10.7	45	29.0	30.2±0.5	44	30.0	30.6±0.4
	12.5	41	28.0	28.0±0.4	47	28.0	28.0±0.4
	14.7	42	28.0	28.2±0.4	40	28.0	29.1±0.8
35	11.3	2	49.0	49.0±4.0	2	42.0	42.0±1.0
	11.7	23	35.0	35.2±1.0	53	31.0	31.4±0.5
	14.3	19	38.0	37.9±1.2	26	38.0	38.3±1.4

Table 5
Adult weight (mg) of *P. interpunctella* reared on split maize kernels

Temp (°C)	Moisture content (%)	Males			Females		
		N	Median	Mean±SE	*N*	Median	Mean±SE
20	11.7	50	9.235	9.072±0.145	46	13.680	13.221±0.331
	13.4	39	9.620	9.083±0.303	40	13.865	13.370±0.517
	14.8	45	8.990	9.114±0.270	40	14.590	14.146±0.320
25	11.0	40	8.300	8.202±0.182	32	12.985	12.558±0.441
	12.7	32	8.360	8.675±1.388	42	13.405	13.069±0.294
	14.8	46	8.240	8.108±0.295	43	13.700	12.841±0.400
30	10.7	45	6.990	6.858±1.116	44	10.595	10.274±0.264
	12.5	41	7.870	7.753±0.201	47	10.950	10.363±0.375
	14.7	42	7.875	7.640±0.213	40	12.610	12.610±0.435
35	11.3	2	3.520	3.520±0.470	2	8.450	8.450±0.950
	11.7	23	6.520	6.239±0.274	53	9.690	9.496±0.223
	14.3	19	5.553	5.553±0.293	26	7.250	7.540±0.302

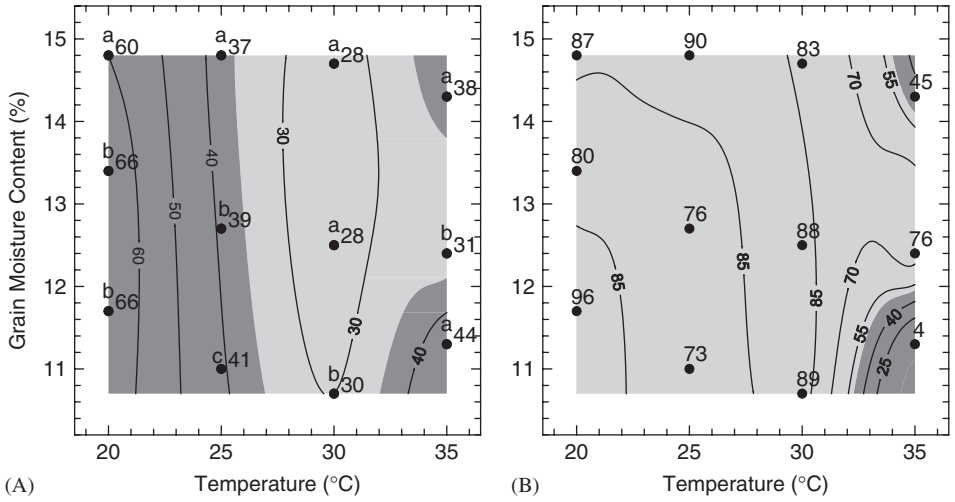

Fig. 2. Influence of temperature and grain moisture content on development of *P. interpunctella* from oviposition to adult eclosion on split maize kernels. (A) Contours of median developmental period in days for males and females combined. Dark shading indicates combinations of temperature and moisture at which the predicted developmental period is 35 d or more. Within each temperature, observed values of median developmental period accompanied by the same letter are not significantly different (Dunn's test, $P<0.05$). (B) Contours of median percentage survival for males and females combined. Dark shading indicates combinations of temperature and moisture at which predicted survival is 50% or less.

with decreasing temperature – more rapidly at low than at high moisture content – and also with increasing temperature. As temperature increases above the optimum, the developmental period increases much more rapidly at high or low moisture contents than at intermediate levels. Survivorship is above 70% at all moisture contents when temperature is $\leqslant 31\,^{\circ}C$, but there is no clear pattern of variation over this range (Fig. 2(B)). As temperature increases to 35 °C, however, survival declines rapidly at both high and low moisture levels.

4. Discussion

The failure of most eggs to hatch at 15 °C, even though embryonic development occurred in many, suggests that 15 °C is near the lower temperature limit for egg development. This is in close agreement with Bell (1975), who found that the eggs of two *P. interpunctella* strains, one from Belgium and one from the UK, failed to hatch at 15 °C, and with Johnson et al. (1995), who estimated a lower threshold of 14.8 °C for egg development in two additional strains from California. Cox and Bell (1991) gave 35 °C as the maximum temperature for development of *P. interpunctella*. Although *P. interpunctella* did complete development at 35 °C in the present study, the increase in developmental period as temperature approached 35 °C Fig. 1(B)), as well as reduced survival at this temperature (Table 5), indicated that 35 °C is, in fact, near the upper limit for development. An increase in developmental period between 30 and 35 °C was also evident in data presented by Mbata and Osuji (1983) for *P. interpunctella* feeding on groundnuts.

Abdel-Rahman et al. (1968) studied development of *P. interpunctella* on whole kernels of nine maize varieties and reported mean developmental periods (egg to adult) ranging from 28.4 to 35.3 d at 27 °C and 70% or 80% r.h. This is in reasonable agreement with the results of the present study, which predict a developmental period of 34.5 d on Pioneer 3320 at 27 °C (Fig. 1B). Mbata (1990) reported developmental periods (larva to adult) ranging from 25.9 to 38.0 d on broken kernels of 13 maize varieties at 30 °C and 70% r. h. The time predicted for development from larva to adult at 30 °C on Pioneer 3320 (Figs. 1(A and B)) falls within this range.

Plodia interpunctella, like many other pests of stored products, has a broad host range but does not develop equally well on all its hosts (Arbogast et al., 2005). This was well illustrated in the present study by the difference in developmental period and adult weight between moths reared on the laboratory diet and those reared on split maize kernels. The range of variation among various host commodities has been well documented by earlier studies, including studies of mixed diets of wheatfeed and glycerine (Prevett, 1971) or wheatfeed, glycerine and dried yeast (Bell, 1975); groundnuts (Mbata and Osuji, 1983); maize varieties (Mbata, 1990; Abdel-Rahman et al., 1968); bran, nuts, and dried fruit (Johnson et al., 1992, 1995); baking ingredients (Locatelli and Biglia (1995); wheat and buckwheat (Locatelli and Limonta, 1998); dried vegetable products (Na and Ryoo, 2000) and seed garlic Perez-Mendoza and Aguilera-Peña, 2004).

Johnson et al. (1992) noted the challenge to population modeling posed by insects, such as *P. interpunctella*, that attack a broad range of hosts differing widely in their ability to support population growth. Yet, meaningful progress can be made toward this end by correcting deficiencies in the biological database for storage pests. The nature of these deficiencies and the research needed to fill the gaps were described by Throne (1995).

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